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Interspecific competition between two parasitoids of *Helicoverpa zea*: *Eucelatoria bryani* and *E. rubentis*

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Abstract

Multiple parasitism of *Helicoverpa zea* (Lepidoptera: Noctuidae) had differential effects on the gregarious endoparasitoids *Eucelatoria bryani* and *E. rubentis* (Diptera: Tachinidae). Both species were able to survive in multiparasitized hosts. However while the survival of *E. bryani* was not affected by the presence of *E. rubentis, E. rubentis* survival was reduced when competing with 24-h older *E. bryani.* The presence of *E. rubentis* did not result in a decrease in the size of *E. bryani* except when *E. rubentis* was 24-h older than *E. bryani.* The presence of *E. bryani* tended to result in smaller *E. rubentis.* The presence of similarly aged heterospecific competitors often resulted in prolonged development time for both species. Naïve females did not alter oviposition between unparasitized and heterospecifically parasitized fifth-instar larvae of *H. zea,* either by ovipositing less frequently in parasitized hosts than unparasitized ones, or by reducing clutch size in parasitized hosts. These results indicate that in *H. zea, E. bryani* is a superior competitor compared with *E. rubentis.* These factors should be considered in evaluating the potential of *E. bryani* and *E. rubentis* as biological control agents of *H. zea.*

Introduction

A key component in determining the success or failure of different species of parasitoids as biological control agents is how those species interact with one another (Zwölfer et al., 1976; Ehler & Hall, 1982). Intrinsically superior parasitoids can eliminate inferior species by out-competing them for host resources, and altering host-parasitoid population dynamics (Hassell, 1986), thereby potentially disrupting control of one or more pest species (Levins & Wilson, 1980; Askew & Shaw, 1986). While tachinid flies (Diptera) have been used successfully as biological control agents (Greathead, 1986), and methods are being developed for their mass production and release (Nettles et al., 1980; Gross & Johnson, 1985; Bratti, 1990; Nettles, 1990; Bratti & Nettles, 1992), little information exists on larval competitive and host discrimination abilities of tachinids.

Eucelatoria bryani Sabrosky and *E. rubentis* (Coquillett) (Diptera: Tachinidae) are facultatively gregarious endoparasitoids of larval Noctuidae (Lepidoptera), and are potentially valuable biological control agents of *Helicoverpa zea* (Boddie) and *Heliothis virescens* (F.) (Lepidoptera: Noctuidae) (Knipling, 1992). *E. bryani* and *E. rubentis* are sympatric across south-central USA and northeastern Mexico. The geographic range of *E. bryani* extends from western Arkansas and eastern Oklahoma south and west to Arizona and Mexico (Jackson et al., 1969; Young & Price, 1975; Sabrosky, 1981; Steward et al., 1990), where it mainly parasitizes *H. zea* and *H. virescens. E. bryani* has previously been referred to as *E. armigera* and *E.* sp. near *armigera.* The present use of the name *E. bryani* is based on the work of Sabrosky (1981). *E. rubentis* occurs across southeastern USA from Delaware to Arkansas south through Florida and west to Texas and Taumalipas, Mexico (Sabrosky, 1981). *E. rubentis* has a broader host range than *E. bryani* (Jackson et al., 1969; Arnaud, 1978; Sabrosky, 1981; Reitz, unpubl.) but is a regular parasitoid of *H. zea*

(Roach, 1975; Hughes & Rabb, 1976; J. D. Culin [Clemson University], pers. comm.).

The present study examines the effect of interspecific competition on the development and survival of *E. bryani* and *E. rubentis*, and if oviposition patterns differ between unparasitized and heterospecifically parasitized hosts. The faster development of *E. bryani* should give it an intrinsic competitive advantage over *E. rubentis* (Reitz, 1994). Therefore if the presence of heterospecific larvae adversely impacts the other species, females may oviposit less in parasitized hosts compared with those ovipositing in healthy hosts. *E.* spp. females adjust primary clutch size in response to certain host attributes, such as size and development stage (Reitz & Adler, 1995; Reitz, unpubl.).

Specifically, I determined which species is the superior larval (intrinsic) competitor by comparing mortality, weights, and development times of parasitoid progeny among different parasitization treatments. I examined three different time intervals between parasitizations: (1) the second parasitoid ovipositing <2 min after the primary parasitoid; (2) the second parasitoid ovipositing 6 h after the primary parasitoid; and (3) the second parasitoid ovipositing 24 h after the primary parasitoid. The maximum interval of 24 h was used so secondary parasitoids would encounter hosts containing first instars of the initial parasitoid (Reitz, 1994). Both *E. bryani* and *E. rubentis* served as primary parasitoid and second parasitoid. Hosts singly parasitized by *E. bryani* and *E. rubentis* served as control groups.

Materials and methods

All insects were reared in an environmental chamber maintained at 26 ± 2 °C, 60 ± 10% r.h., L14:D10. *E. bryani* and *E. rubentis* were reared according to methods outlined by Nettles et al. (1980) and Reitz & Adler (1991). Parasitoid females were 10–15 days old when used for parasitization and had no prior oviposition experience. Females were isolated for approximately 2 h before oviposition and were used only once. *H. zea* larvae were reared individually in 30-ml plastic diet cups, on a pinto bean – wheat germ diet (Burton, 1969, as modified in Adler & Adler, 1988). All *H. zea* larvae used in these tests were feeding-stage fifth instars (Webb & Dahlman, 1985).

For parasitization, each *H. zea* larva was held behind the head capsule, with soft forceps and presented directly to an individual female parasitoid. Each female was allowed to oviposit once. Oviposition can be detected by the presence of a drop of hemolymph on the host cuticle following attack. If a female did not oviposit within 2 min, the trial was terminated. The eight parasitization treatments are designated as:

1. B: Single parasitization by *E. bryani*
2. BR-0: Parasitization by *E. bryani* followed immediately (<2 min) by *E. rubentis*.
3. BR-6: Parasitization by *E. bryani* followed by *E. rubentis*, 6 h later.
4. BR-24: Parasitization by *E. bryani* followed by *E. rubentis*.
5. R: Single parasitization by *E. rubentis*.
6. RB-0: Parasitization by *E. rubentis* followed immediately (<2 min) by *E. bryani*.
7. RB-6: Parasitization by *E. rubentis* followed by *E. bryani*, 6 h later.
8. RB-24: Parasitization by *E. rubentis* followed by *E. bryani*, 24 h later.

Nine days after parasitization, all parasitoid puparia were weighed individually to the nearest 0.1 mg. The species, sex, and date of emergence were recorded for each fly. All *H. zea* larvae were dissected to determine the number and stage-specific mortality of *E.* spp. immatures. The three larval instars of *E. bryani* and *E. rubentis* are distinguished by the size and shape of the cephalopharyngeal apparatus. In addition, any puparia that did not produce adult flies were dissected to determine species and developmental condition. The sum of adults and dead immatures of each parasitoid species per host constitutes the primary clutch size.

For each host, the difference between primary (number of eggs in a clutch) and secondary clutches (number of adults) was used as an index of mortality. I tested for differences in mortality among the seven parasitization treatments for each species by ANOVA and used a test of independence to determine if stage-specific mortality of the parasitoids was dependent on parasitization treatment.

The presence of heterospecific competitors may affect the development and weight of *E.* spp. progeny. Because size and development time differ between these parasitoid species and sexes, differences in progeny weights and development times among the parasitization treatments were analyzed separately for the four species – sex combinations. To determine if the presence of heterospecific competitors affects development time independently of parasitoid size, I correlated puparial weight with development time for each treatment. Weights and development times are based on the mean per host for each species – sex combination. These analyses include only puparia that produced adult parasitoids.

To determine if oviposition by the second species differed between unparasitized and previously parasitized hosts, data were analyzed in two ways. For both analyses, all hosts where a species acted as the primary parasitoid were pooled and compared to the three treatments where that species acted as the second parasitoid. To determine if parasitized hosts were rejected for oviposition more frequently than unparasitized hosts, oviposition was treated as a simple dichotomy based on the presence of parasitoids. The resulting 2 response $\times$ 4 treatment contingency table was analyzed with a test of independence for each species. Because *E. bryani* and *E. rubentis* can adjust their primary clutch size (number of eggs deposited in a host), they may oviposit in previously parasitized hosts but deposit smaller clutches in parasitized hosts than unparasitized hosts. Therefore, to determine if primary clutch size differs in response to parasitism condition of the host, differences in primary clutch sizes between unparasitized and previously parasitized hosts were analyzed via an analysis of variance (ANOVA).

Analyses are based on transformed data where appropriate. Means and standard errors are given for untransformed data. Because of the different analyses performed on the data, a 1% probability level was used to determine statistical significance.

Results

E. bryani mortality was not related to the presence of *E. rubentis* ($F=0.92$, df$=6$, 197, $P>0.48$, $\sqrt{}(y+0.375)$ transformed data), even when *E. rubentis* had a 24 h headstart in development (Figure 1). Stage-specific mortality for *E. bryani* was independent of parasitization treatment ($G=26.2$, df$=18$, $P=0.10$).

E. rubentis mortality was affected by the presence of *E. bryani* ($F=8.50$, df$=6$, 184, $P<0.0001$). *E. rubentis* mortality was significantly higher in hosts parasitized by *E. bryani* 24 h previously (BR-24) than in hosts in other treatment groups (Figure 2). Stage-specific mortality for *E. rubentis* was dependent on parasitization treatment ($G=62.2$, df$=18$, $P<0.0001$). The greatest mortality for *E. rubentis* occurred in the BR-24 group, and within that group, mortality was greatest (80%) among second-instar maggots ($n=30$).

For *E. bryani* progeny, puparial weights of females differed significantly among the seven treatment groups ($F=4.81$, df$=6$, 136, $P<0.001$, log-transformed data; Table 1). Puparia from the RB-24 treatment weighed significantly less than those from all other parasitization treatments, except for the RB-0 group. However, puparia from the RB-0 group did not weigh significantly less than puparia from the other groups. There were no other significant differences in mean weights among the five other treatment groups (Table 1). *E. bryani* male puparia also varied in weight among the treatment groups ($F=5.18$, df$=6$, 125, $P<0.0001$). As with *E. bryani* females, *E. bryani* male puparia in the RB-24 group weighed less than those of most other groups (Table 1). Otherwise, the presence of *E. rubentis* did not have an adverse impact on *E. bryani* males. In fact, *E. bryani* males in the RB-6 group were significantly heavier than ones in the control (B) group.

For *E. rubentis* progeny, puparial weights of females also showed significant differences among the treatment groups ($F=4.97$, df$=6$, 110, $P<0.001$). *E. rubentis* females could be separated into two groups on the basis of weight. The heavier puparia were from the control group (R) or the treatments groups where *E. rubentis* parasitized hosts at least 6 h before *E. bryani* (i.e., RB-6, RB-24; Table 2). Although *E. rubentis* females from the BR-24 group were over 5 mg (19%) lighter than females from the groups where *E. rubentis* had parasitized the host at least 6 h before *E. bryani*, the small sample size in the BR-24 group precluded a meaningful statistical comparison. The small sample size resulted from the high mortality (79%) of *E. rubentis* in the BR-24 group. Puparial weights of *E. rubentis* males varied in a pattern similar to that of *E. rubentis* females ($F=6.18$, df$=6$, 119, $P<0.0001$). The largest *E. rubentis* males were from hosts singly parasitized by *E. rubentis* (R) and those parasitized by *E. rubentis* at least 6 h before *E. bryani* (i.e., RB-6, RB-24; Table 2). Again, disparate sample sizes caused by the greater *E. rubentis* mortality distorted the results.

Development times for *E. bryani* females varied across treatments ($F=11.59$, df$=6$, 136, $P<0.0001$), but the variation did not correspond to the variation in *E. bryani* female weights (Table 1). As expected by their smaller size, *E. bryani* females in the RB-24 group had the shortest development time. However, these times were not significantly different from the development time for *E. bryani* females in the BR-24 group. Development times for *E. bryani* males also differed across the treatments ($F=5.86$, df $=6$, 125, $P<0.0001$). Males in the RB-24 group emerged one day before males in the control (B) group (Table 1).

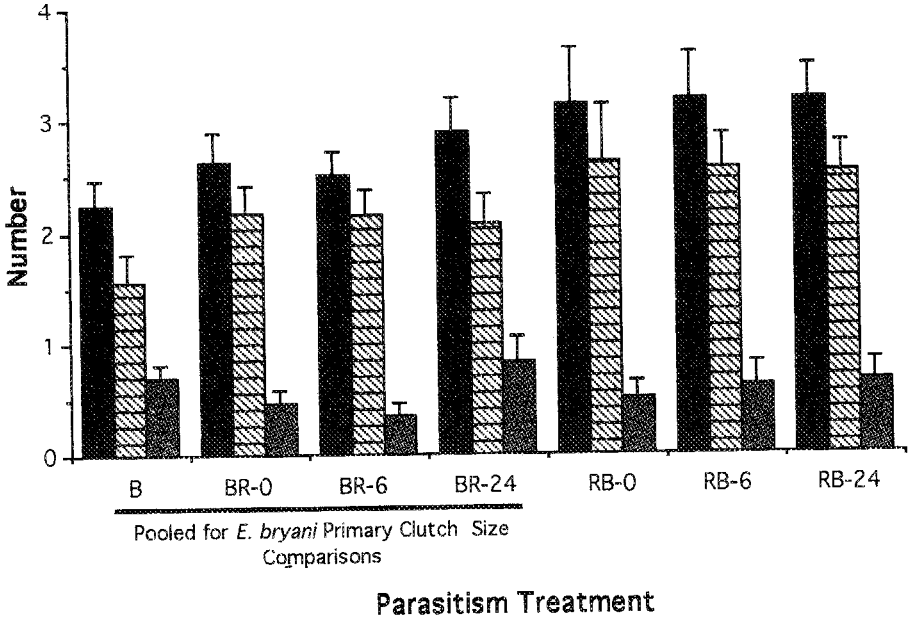

Figure 1. Eucelatoria bryani mean number of eggs (■), adults (▧), and mortality (▤), difference between number of eggs and adults) in singly and multiply parasitized *Helicoverpa zea*. For *E. bryani* primary clutch size (number of eggs) comparisons, B, BR-0, BR-6, and BR-24 treatments were pooled. Vertical lines on each bar represent standard errors.

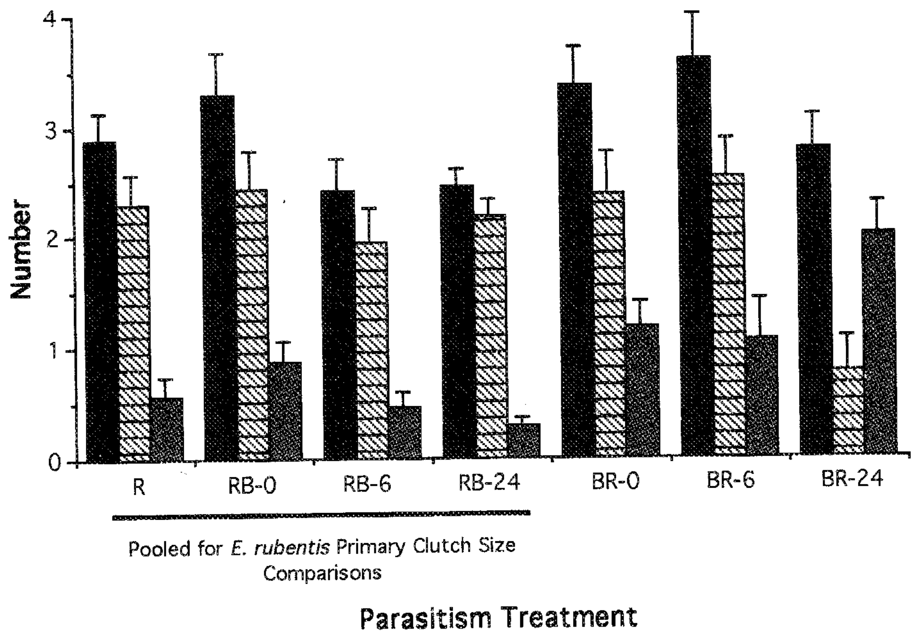

Figure 2. Eucelatoria rubentis mean number of eggs (■), adults (▧), and mortality (▤, difference between number of eggs and adults) in singly and multiply parasitized *Helicoverpa zea*. For *E. rubentis* primary clutch size (number of eggs) comparisons, R, RB-0, RB-6, and RB-24 treatments were pooled. Vertical lines on each bar represent standard errors.

Alternatively, males from hosts where there was no delay between primary parasitization and secondary parasitization (i.e., BR-0 and RB-0) emerged about 1 day after males in the control (B) group. As with *E. bryani* females, development times for *E. bryani*

Table 1. Puparial weights and development times (mean ± SE), and their correlations for *Eucelatoria bryani* females and males. Values are based on the mean for each sex per *Helicoverpa zea* host. Means followed by the same letter, within a column, are not significantly different (P>0.01, LSMeans t-test)

Treatment	Females n	Females Puparial weight (mg)	Females Development time (days)	Females r^a	Males n	Males Puparial weight (mg)	Males Development time (days)	Males r^a
B	44	26.01 ± 0.56a	12.2 ± 0.13a	0.48*	41	24.96 ± 0.57a	11.6 ± 0.13a	0.61*
BR-0	19	25.98 ± 0.86a	13.2 ± 0.20b	0.22 NS	18	27.31 ± 0.99ab	12.8 ± 0.22bc	0.06 NS
BR-6	11	28.61 ± 1.18a	12.4 ± 0.27a	−0.38 NS	12	27.94 ± 1.24ab	12.1 ± 0.27abc	0.47 NS
BR-24	11	28.41 ± 1.22a	11.6 ± 0.28ac	0.16 NS	9	24.71 ± 1.37abc	11.2 ± 0.30ad	0.02 NS
RB-0	20	24.81 ± 0.84ab	12.7 ± 0.19ab	0.40 NS	17	25.44 ± 0.85ab	12.5 ± 0.19c	0.07 NS
RB-6	14	27.63 ± 0.95a	12.4 ± 0.22ab	−0.16 NS	15	28.97 ± 1.08b	12.1 ± 0.24abc	0.10 NS
RB-24	24	22.80 ± 0.76b	11.3 ± 0.17c	0.52 *	20	22.05 ± 0.85c	10.6 ± 0.19d	0.55 *

^{a}* - Pearson correlation coefficient P<0.01, NS - Pearson correlation coefficient P>0.01.

Table 2. Puparial weights and development times (mean ± SE), and their correlations for *Eucelatoria rubentis* females and males. Values are based on the mean for each sex per *Helicoverpa zea* host. Means followed by the same letter, within a column, are not significantly different (P>0.01, LSMeans t-test)

Treatment	Females n	Females Puparial weight (mg)	Females Development time (days)	Females r^a	Males n	Males Puparial weight (mg)	Males Development time (days)	Males r^a
R	38	29.82 ± 0.75a	13.0 ± 0.15a	0.57*	36	31.16 ± 0.91a	12.7 ± 0.16a	0.53*
RB-0	19	24.35 ± 1.00b	13.1 ± 0.20ac	0.55 NS	19	26.17 ± 1.10b	12.8 ± 0.20a	0.53 NS
RB-6	7	29.23 ± 1.65a	12.9 ± 0.33abc	0.84 NS	14	31.39 ± 1.43ac	12.7 ± 0.26a	0.52 NS
RB-24	19	29.00 ± 1.16a	12.0 ± 0.23b	0.77 *	21	30.85 ± 1.17ac	11.9 ± 0.21b	0.54 *
BR-0	18	24.15 ± 1.19b	13.7 ± 0.24c	0.18 NS	18	26.12 ± 1.05b	13.2 ± 0.19a	0.18 NS
BR-6	14	26.21 ± 1.31ab	13.4 ± 0.26ac	0.37 NS	12	26.63 ± 1.10bc	12.4 ± 0.25ab	0.57 NS
BR-24	2	24.25 ± 3.01‡	11.3 ± 0.17‡	‡	6	22.83 ± 2.02b	11.4 ± 0.36b	0.48 NS

^{a} * - Pearson correlation coefficient P<0.01, NS - Pearson correlation coefficient P>0.01.
‡ Not included in multiple comparisons.

males in the BR-24 group were similar to those for the control (B) group and the RB-24 group.

Development times for *E. rubentis* also varied across treatment groups (females: F=5.76, df=6, 110, P<0.0001; males: F=5.69, df=6, 119, P<0.0001, Table 2). Similar to the pattern for *E. bryani*, the fastest developing *E. rubentis* progeny were from hosts where *E. rubentis* parasitized hosts 24 h after *E. bryani* (i.e., BR-24). Development times also tended to be shorter for *E. rubentis* in the RB-24 group.

Development times for both *E. bryani* and *E. rubentis* were affected by the presence of heterospecific competitors, independent of parasitoid weight. In all four of the control groups, puparial weights were positively correlated with development time (Tables 1 and 2). However, when there was no more than a 6 h delay between parasitizations, puparial weights and development times were not correlated.

Both species readily parasitized heterospecifically parasitized hosts. *E. bryani* females oviposited in parasitized hosts as frequently as in unparasitized ones (G=1.7, df=3, P=0.63). *E. bryani* females oviposited in 79% of unparasitized hosts (n=164), 86% of RB-0 hosts (n=35), 75% of RB-6 hosts (n=24), and 74% of RB-24 hosts (n=39). In hosts where *E. bryani* did oviposit, *E. bryani* females did not adjust primary clutch size in response to parasitization condition of hosts (F=1.53, df=3, 200, P=0.021, $\surd$(y+0.375) transformed data; Figure 1). The mean primary clutch size for *E. bryani* when acting as the primary parasitoid was 2.59±0.147.

E. rubentis females also did not show discrimination against previously parasitized hosts (G = 8.2, df = 3, P = 0.042). *E. rubentis* parasitized 74% of unparasitized hosts (n = 172), 73% of BR-0 hosts (n = 37) and 67% of BR-6 hosts (n = 27), and 50% of the BR-24 hosts (n = 36). In hosts that *E. rubentis* did parasitize, *E. rubentis* primary clutch size did not differ according to parasitization condition of the host (F = 2.50, df = 3, 185, P>0.06, Figure 2). The primary clutch size for *E. rubentis* when acting as a primary parasitoid was 2.73 ± 0.138.

Discussion

Multiple parasitism of *H. zea* incurs certain costs to progeny of both *E. bryani* and *E. rubentis*. These costs to second parasitoid progeny increase with the interval between ovipositions. *E. bryani* is the superior intrinsic competitor compared with *E. rubentis*, and the presence of *E. rubentis* had relatively minor impacts on *E. bryani*. In contrast, the presence of *E. bryani* represents a significant cost to *E. rubentis*, in the form of greater mortality, reduced weight, and altered development time. Interactions between *E. bryani* and *E. rubentis* larvae are of an indirect scramble-type competition because there was no evidence that maggots of either species physically attacked one another or that *E. bryani* physiologically suppressed *E. rubentis* directly. Therefore the competitive advantage *E. bryani* has over *E. rubentis* probably results from the faster development rate of *E. bryani* (Reitz, 1994).

Multiple parasitism among the Tachinidae usually results in the survival of one species, usually the first species that parasitizes a host (Mellini, 1990). As the present results demonstrate, multiple parasitism can affect other aspects of parasitoid fitness in addition to mortality. Another aspect of fitness is potential fecundity, which in *E. bryani* and *E. rubentis*, as in other parasitoids, is correlated with size (Reitz, 1994; Reitz & Adler, 1995). In terms of progeny size, *E. bryani* was at a disadvantage only when *E. rubentis* larvae were 24 h older than *E. bryani*. Otherwise, *E. bryani* progeny from multiply parasitized hosts were as large as, or larger than, *E. bryani* from singly parasitized hosts. Conversely, *E. rubentis* progeny tended to be smaller when competing with *E. bryani*, except when *E. rubentis* were at least 6 h older than *E. bryani*.

The largest effect *E. rubentis* competitors had on *E. bryani* was on its development time. When the interval between ovipositions was short (≤6 h), development times, especially for males, tended to be longer than for singly parasitized hosts. A similar pattern held for *E. rubentis* development times. In these shorter intervals between ovipositions, the prolonged development may reflect interference from competitors (Pschorn-Walcher, 1971; McBrien & Mackauer, 1990) or anoxia (King et al., 1976) that results in a longer time to garner sufficient resources. There may be a time interval at which *E. rubentis* larvae, as second parasitoids, have no appreciable effect on *E. bryani*. When *E. bryani* larvae were 24 h older than *E. rubentis*, the development time of *E. bryani* was not significantly different from that of singly parasitized hosts. Conversely, while the shortened development time for second parasitoid progeny, when 24 h younger than initial parasitoid progeny, might simply reflect the smaller size of those progeny, the smaller size may result from a scarcity of host resources or degradation of the host by the older, initial parasitoid species. During the second and third stadia, tachinid larvae secrete proteolytic enzymes into the host hemocoel for extra-intestinal digestion, which decompose the viscera of the host (Mellini, 1990).

The frequency of oviposition and primary clutch size of *E. bryani* and *E. rubentis* indicate that naïve females of either species did not distinguish between hosts being parasitized or unparasitized. Given the relatively minor impact of *E. rubentis* on *E. bryani*, discrimination between unparasitized and heterospecifically parasitized hosts within the first 24 h following parasitism, is not necessary for *E. bryani*. *E. rubentis* females did not respond to this aspect of host quality, as they do to other aspects such as size or development stage (Reitz & Adler, 1995; Reitz, 1994) although the presence of *E. bryani* represents a significant cost to *E. rubentis* progeny. While *E. rubentis* did not demonstrate host discrimination under the present conditions, the decision to behave differently towards parasitized and unparasitized hosts is influenced by other factors, including prior oviposition experience, host availability, or egg load (Bakker et al., 1985; van Alphen & Visser, 1990). Differential behavior towards parasitized and unparasitized hosts can be expected to occur when multiple parasitism reduces the fitness of the progeny of a secondary parasitoid in multiparasitized hosts compared with singly parasitized hosts. For example, *Myiopharus doryphorae* (Riley) and *M. aberrans* (Townsend) rarely oviposit in conspecifically parasitized hosts because *Myiopharus* are solitary species where only one larva per host will survive (López et al., 1995), but strategies for the gregarious *E. bryani* and *E. rubentis* probably differ.

Under the same laboratory conditions as the present study, over 60% of *E. bryani* molted to the second instar within 24 h of oviposition, roughly corresponding to the 50% of BR-24 hosts in which *E. rubentis* did not oviposit. In contrast, the slower developing *E. rubentis* does not molt to the second instar until 24–36 h following oviposition (Reitz, 1994). Therefore, *E.* spp. females might alter oviposition upon encountering hosts containing older parasitoid larvae, where their progeny would be less likely to survive. Oviposition, which can be rapid (occurring in less than 2 sec), consists of the female approaching a host, then standing on the dorsum of the host, where the parasitoid may use her forelegs to palpate the host, and finally oviposition (Reitz, unpubl.). Females of both species oviposit directly in the host by piercing the host cuticle with a triangular-shaped sternotheca. Despite the brevity of oviposition bouts, females can adjust primary clutch size (number of eggs deposited in a host) in proportion to host size at the time of parasitization (Reitz & Adler, 1995). Other parasitoids base oviposition decisions on external cues of host condition (Strand & Vinson, 1983; Schmidt & Smith, 1985; McBrien & Mackauer, 1990), and parasitized *H. zea* do show pathological signs that are correlated with parasitoid development (Reitz & Nettles, 1994). However, these parasitism-related changes in host condition may not be pronounced enough when *E.* spp. maggots are hematophagous first-instars to be detected by potential second parasitoid females.

Multiple parasitism of *H. zea* by *E. bryani* and *E. rubentis* does incur certain costs to both parasitoid species, with the costs being greater for *E. rubentis* than for *E. bryani*. Further investigations are needed to determine when the benefits of multiple parasitism outweigh the costs for *E. bryani* and *E. rubentis*. Given the competitive advantage that *E. bryani* has over *E. rubentis* when parasitizing *H. zea*, the effects of frequent multiple parasitism between these closely related species on their population dynamics, and on the population dynamics of their hosts need to be considered in evaluating the use of *E. bryani* or *E. rubentis* in biological control programs.

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References

Adler, P. H. & C. R. L. Adler, 1988. Behavioral time budget for larvae of *Heliothis zea* (Lepidoptera: Noctuidae) on artificial diet. Annals of the Entomological Society of America 81: 682–688.

Alphen, J. J. M. van & M. E. Visser, 1990. Superparasitism as an adaptive strategy for insect parasitoids. Annual Review of Entomology 35: 59–79.

Arnaud, P. H., Jr., 1978. A host-parasite catalog of North American Tachinidae (Diptera). United States Department of Agriculture Science and Education Administration Miscellaneous Publication, no. 1319.

Askew, R. R. & M. R. Shaw, 1986. Parasitoid communities: their size, structure and development. In: J. Waage & D. Greathead (eds), Insect Parasitoids. Academic Press, London: 225–264.

Bakker, K., J. J .M. van Alphen, F. H. D. van Batenburg, N. van der Hoeven, H. W. Nell, W. T. F. H. van Strien-van Liempt & T. J. C. Turlings, 1985. The function of host discrimination and superparasitism in parasitoids. Oecologia 67: 572–576.

Bratti, A., 1990. Tecniche di allevamento in vitro per gli stadi larvali di insetti entomofagi parassitoidi. Bolletino Istituto Entomologia Universitá Bologna 44: 169–220.

Bratti, A. & W. C. Nettles, Jr., 1992. In vitro rearing of *Eucelatoria bryani* – improvements and evaluation of factors affecting efficiency. Entomologia Experimentalis et Applicata 63: 213–219.

Burton, R. L., 1969. Mass rearing the corn earworm in the laboratory. United States Department of Agriculture, Agricultural Research Service 33–134.

Ehler, L. E. & R. W. Hall, 1982. Evidence for competitive exclusion of introduced natural enemies in biological control. Environmental Entomology 11: 1–4.

Greathead, D. J., 1986. Parasitoids in classical biological control. In: J. Waage & D. Greathead (eds), Insect Parasitoids. Academic Press, London: 290–318.

Gross, H. R., Jr. & R. Johnson, 1985. *Archytas marmoratus* (Diptera: Tachinidae): advances in large-scale rearing and associated biological studies. Journal of Economic Entomology 78: 1350–1353.

Hassell, M. P., 1986. Parasitoids and population regulation. In: J. Waage & D. Greathead (eds), Insect Parasitoids. Academic Press, London: 201–224.

Hughes, P. S. & R. L. Rabb, 1976. A survey of tachinid parasites of *Heliothis zea* and *Heliothis virescens* in North Carolina. Journal of the Georgia Entomological Society 11: 259–265.

Jackson, C. G., D. E. Bryan & R. Patana, 1969. Laboratory studies of *Eucelatoria armigera*, a tachinid parasite of *Heliothis* spp. Journal of Economic Entomology 62: 907–909.

King, E. G., L. R. Miles & D. F. Martin, 1976. Some effects of superparasitism by *Lixophaga diatraeae* of sugarcane borer larvae in the laboratory. Entomologia Experimentalis et Applicata 20: 261–269.

Knipling, E. F., 1992. Principles of insect parasitism analyzed from new perspectives. Washington, United States Department of Agriculture, Agriculture handbook no. 693.

Levins, R. & M. Wilson, 1980. Ecological theory and pest management. Annual Review of Entomology 25: 287–308.

López, R., D. N. Ferro & R. G. Van Driesche, 1995. Two tachinid species discriminate between parasitized and non-parasitized hosts. Entomologia Experimentalis et Applicata 74: 37–45.

McBrien, H. & M. Mackauer, 1990. Heterospecific larval competition and host discrimination in two species of aphid parasitoids: *Aphidius ervi* and *Aphidius smithi*. Entomologia Experimentalis et Applicata 56: 145–153.

Mellini, E., 1990. Sinossi di biologia dei Ditteri Larvevoridae. Bolletino Istituto Entomologia Universitá Bologna 45: 1–38.

Nettles, W. C., 1990. In vitro rearing of parasitoids – role of host factors in nutrition. Archives of Insect Biochemistry and Physiology 13: 167–175.

Nettles, W. C., Jr. C. M. Wilson & S. W. Ziser, 1980. A diet and method for the *in vitro* rearing of the tachinid, *Eucelatoria* sp. Annals Entomological Society of America 73: 180–184.

Pschorn-Walcher, H., 1971. Experiments on inter-specific competition between three species of tachinids attacking the sugar cane moth borer, *Diatraea saccharalis* (F.). Entomophaga 16: 125–131.

Reitz, S. R., 1994. Reproductive biology of *Eucelatoria bryani* and *Eucelatoria rubentis* (Diptera: Tachinidae), larval parasitoids of *Helicoverpa zea* (Lepidoptera: Noctuidae). Ph. D. Thesis, Clemson University.

Reitz, S. R. & P. H. Adler, 1991. Courtship and mating behavior of *Eucelatoria bryani* (Diptera: Tachinidae), a larval parasitoid of *Heliothis* spp. (Lepidoptera: Noctuidae). Annals of Entomological Society of America 84: 23–30.

Reitz, S. R. & P. H. Adler, 1995. Fecundity and oviposition of *Eucelatoria bryani*, a gregarious parasitoid of *Helicoverpa zea* and *Heliothis virescens*. Entomologia Experimentalis et Applicata 75: 175–181.

Reitz, S. R. & W. C. Nettles, Jr., 1994. Regulation of *Helicoverpa zea* larval behavior by the parasitoid *Eucelatoria bryani*. Entomologia Experimentalis et Applicata 71: 33–39.

Roach, S. H., 1975. *Heliothis* spp.: larvae and associated parasites and diseases on wild host plants in the Pee Dee area of South Carolina. Environmental Entomology 4: 725–728.

Sabrosky, C. W., 1981. A partial revision of the genus *Eucelatoria* (Diptera: Tachinidae), including important parasites of *Heliothis*. United States Department of Agriculture Technical Bulletin, no. 1635, 18 pp.

Schmidt, J. M. & J. J. B. Smith, 1985. Host volume measurement by the parasitoid wasp *Trichogramma minutum*: the role of curvature and surface area. Entomologia Experimentalis et Applicata 39: 213–221.

Steward, V. B., W. C. Yearian & T. J. Kring, 1990. Parasitism of *Heliothis zea* (Lepidoptera: Noctuidae) eggs on grain sorghum panicles. Environmental Entomology 19: 154–161.

Strand, M. R. & S. B. Vinson, 1983. Factors affecting host recognition and acceptance in the egg parasitoid *Telenomus heliothidis* (Hymenoptera: Scelionidae). Environmental Entomology 12: 1114–1119.

Webb, B. A. & D. L. Dahlman, 1985. Developmental pathology of *Heliothis virescens* larvae parasitized by *Microplitis croceipes*: parasite-mediated host developmental arrest. Archives of Insect Biochemistry and Physiology 2: 131–143.

Young, W. R. & R. G. Price, 1975. Incidence, parasitism, and distribution patterns of *Heliothis zea* on sorghum, cotton, and alfalfa for southwestern Oklahoma. Environmental Entomology 5: 777–779.

Zwölfer, H., M. A. Ghani & V. P. Rao, 1976. Foreign exploration and importation of natural enemies. In: C. B. Huffaker & P. S. Messenger (eds), Theory and Practice of Biological Control. Academic Press, New York: 189–207.